artery, a vessel which passes downwards between the sub-cerebral commissure and the broad and short anterior pedal commissure. To some of the arteries with which it is in contact the sub-cerebral commissure seems to give off one or two pairs of very slender nerves.

The sub-cerebral commissure is quite as well developed in these three species as in any of the sigmurethrous snails in which I have observed it, and it is probable that it will be found also in other orthurethrous forms. Indeed, I believe that I have seen it in *Pleurodiscus flavidus* (Rossm.) [= *Patulastra balmei* (P. & M.)] and in *Acanthinula aculeata* (Müll.), although I have not been successful in following it throughout its entire length in these species, and should not yet like to state definitely that it is present. It is very likely, however, that this slender commissure will be found to occur generally throughout the Orthurethra. Thus the evidence now before us would seem to point to the conclusion that in the Pulmonata there are normally five commissures passing beneath the alimentary canal, namely, the buccal commissure, the sub-cerebral commissure, the two pedal commissures, and the visceral commissure; but of these the narrow sub-cerebral is, of course, the only ventral commissure that unites the cerebral ganglia directly, without the intervention of any other ganglia.

SUMMARY.

A slender sub-cerebral commissure is now known to unite the cerebral ganglia beneath the alimentary canal not only in half-a-dozen families of sigmurethrous snails, but also in at least three orthurethrous genera, namely, *Ena*, *Rachis*, and *Chondrina*. It is probable that it is present also in other genera of the Orthurethra, and that there may normally be five ventral commissures in the Pulmonata.

THE ANATOMY AND GENERAL AFFINITIES OF *OCHTHEPHILA* (= *GEOMITRA*) *TURRICULA* (LOWE).

By HUGH WATSON, M.A.

Read 8th June, 1923.

PLATE VI.

(1) ANATOMICAL DESCRIPTION.

THE following account of the anatomy of *Ochthephila* (*Hystricella*) *turricula* (Lowe)[1]—otherwise known as *Geomitra turricula*[2]—is

[1] *Trans. Cambridge Philos. Soc.*, vol. iv, 1831, p. 58, pl. vi, fig. 21.

[2] In 1895 Pilsbry discarded the name *Ochthephila* Beck, 1837, in favour of *Geomitra* Swainson, 1840, because he thought that the former generic name was too like *Ochthiphila*, a name which Fallén had given to a genus of flies in 1823 (see *Man. Conch.*, ser. II, vol. ix, pp. 238, 239, 243). But Pilsbry wrote before the establishment of the International Rules for Zoological Nomenclature; and it is clear from the recommendations of Article 36 of this

based on the examination of some specimens kindly given to me by Mr. A. S. Kennard, to whom I am much indebted for the opportunity of examining this interesting snail. The specimens were collected by Professor T. D. A. Cockerell on the Island of Cima, a small rocky islet off the south-east coast of Porto Santo, about 35 miles north-east of Madeira. The species appears to be confined to this little island, where it occurs in considerable numbers ; but numerous other members of the same genus are found throughout the Madeira Islands, although very little has been published about their anatomy.

The Shell of the specimens examined measures about 9 mm. in height by 6·5 mm. in its greatest diameter. Its form will be seen from Pl. VI, Fig. 1. The whorls are covered with minute oval granules, the major diameter of each individual granule being parallel to the lines of growth on the first two whorls, but horizontal on the remaining whorls. The shell is of a brown colour, the apex and the uninterrupted peristome being pale. Above the periphery the whorls are crossed by ill-defined lighter and darker oblique streaks. On the base of some of the specimens a broad, dark brown band encircles a lighter central area, which is perforated by the very narrow umbilicus.

The Head bears the usual two pairs of tentacles, with the eyes at the ends of the upper pair, and the usual labial palps. The genital opening is situated on the right side of the head, below and a little behind the base of the upper right tentacle, from which it is separated by about ·8 mm. A network of grooves divides the skin of the head and neck into numerous small polygonal rugæ. Vertical facial grooves are absent ; the oblique lateral grooves on the sides of the neck are somewhat irregular and poorly developed ; but the two dorsal grooves are better defined, and are rather close together. A pair of very broad, dark grey bands extends forwards from below the mantle-edge as far as the upper tentacles ; the bands nearly meet dorsally, but leave an unpigmented area beneath them on each side above the edges of the foot. The front of the head is light grey. Where the pigment is present it is chiefly concentrated on the tops of the rugæ, the grooves being paler.

The Foot is bluntly pointed at the hinder end, which is slightly flattened, there being no keel, nor median posterior groove, nor caudal mucous pore. A narrow peripodial groove runs along the edge of the foot, but there is no defined foot-fringe. The sole is unpigmented and is obscurely tripartite, the narrow lateral areas meeting at the posterior extremity, but tapering to a point at the

International Code that a name which only differs from another generic name " in a slight variation in spelling " is " not to be rejected on this account ", even if it is believed to be of the same derivation. Therefore I follow Professor Cockerell in using the name *Ochthephila* Beck, instead of the later name *Geomitra* Swainson, for this genus of snails (*Journ. of Conch.*, vol. xvi, 1922, p. 310).

front end, where the large median area comes to occupy the whole breadth of the sole. The upper surface of the hinder end of the foot is darkly pigmented, the colour in some cases extending right across it, while in other specimens it takes the form of a pair of broad lateral bands passing obliquely downwards from below the mantle.

The Pedal Gland, which opens above the front edge of the foot, extends far back, embedded in the pedal muscles, though the top of its anterior part is exposed to the body-cavity. It consists of very numerous large gland-cells, of which the secretion stains blue with hæmatoxylin, surrounding a central longitudinal duct. The gland measures a little over ·5 mm. in diameter, while the diameter of the duct is about ·14 mm., except close to the opening, where it becomes much broader. Along the floor of the duct there is a pair of wide longitudinal ridges, with a median groove between them, towards which the gland-cells converge. On the outer side of each of these ridges, in the angle between it and the side of the duct, there is a much smaller longitudinal ridge, formed by a thickening of the epithelium lining the duct, this outer pair of ridges consisting of tall narrow columnar cells instead of cubical epithelial cells. The roof of the duct shows some small longitudinal folds.

Numerous small unicellular glands are present in the foot-sole.

The Mantle-Edge is of a pale colour, excepting the upper part near the respiratory opening, where it is often more or less tinged with grey. It bears right and left body-lobes, as shown in Fig. 2 on Plate VI. The right lobe is divided by a deep slit into an elongated portion, which lies near the penultimate whorl, and a small, somewhat quadrate portion lying below the respiratory opening. Two widely separated left body-lobes are present: a little one situated at the base of the aperture, and a larger one situated on the left side of the respiratory opening, and having a small extension which arches over the opening in the manner shown in the drawing.

The Mantle-Cavity is long, and stretches round a complete whorl. Its roof is thin and translucent, but part of it shows minute specks of brown pigment. This pigment is chiefly concentrated to form a brown patch near the mantle-edge behind the respiratory opening; but in some specimens it extends below the periphery to form a short band parallel to and just behind the mantle-edge; while it may also extend backwards for a much greater distance as a faintly pigmented zone between the rectum and the pulmonary vein. The remainder of the skin lining the shell is unpigmented.

The Vascular System.—The main pulmonary vein is large and conspicuous. It receives some small branches towards its anterior end, but these are not at all prominent and can only be seen under a strong lens. Where the pulmonary vein passes beneath the anterior part of the kidney, sections show that it receives a series of minute vessels from the inner surface of that organ. Then, as it passes into the pericardium, it receives three slightly larger branches, one from

the inner and one from the outer surface of the kidney, and one from below the pericardium.

The heart is shown in Fig. 10 on Plate VI. The auricle has an extremely thin wall formed of a pavement epithelium of flattened cells with discoidal nuclei, within which is an open network of muscle-fibres. The walls of the ventricle have a very similar structure, except that the muscle-fibres are far more numerous and the outer ones form a practically continuous layer next to the limiting epithelium. The auriculo-ventricular valve is formed by a pair of small muscular membranes, which project into the cavity of the ventricle where the auricle opens into it and leave only a narrow slit between them.

The aorta divides into anterior and posterior branches soon after leaving the hinder end of the ventricle. The anterior aorta is large; it lies close to the inner side of the spermoviduct for the greater part of its length, but bends away from it in front, passing to the ventral nerve ganglia, where it divides in the usual manner into the odontophoral artery, the pedal artery, etc. The pedal artery can be traced backwards in the foot even beyond the posterior extremity of the pedal gland; it is situated immediately above the duct of the pedal gland for most of its length.

The Excretory System.—The pericardium communicates with the exterior by means of the reno-pericardial duct, the kidney, the ureter, and the mantle-cavity. The reno-pericardial duct projects into the kidney from the inner and upper side of the pericardium about opposite to the middle of the ventricle. (Its position is shown in Fig. 10 on Plate VI.) It consists of a narrow duct, ·33 mm. in length, lined by a strongly ciliated epithelium.

The kidney attains a length of about 5 mm., being rather more than twice as long as the pericardium. Its hinder end extends upwards to the rectum, as shown in Fig. 10. Internally its walls form a spongy network of thin folds covered with excretory cells.

The ureter arises from the extreme front end of the kidney. It then runs backwards along the upper edge of the kidney to the posterior extremity of the mantle-cavity, where it curves round and passes forwards beside the rectum for about ·5 mm. and then opens. The secondary ureter is thus exceedingly short, as will be seen from the figure. In front of the opening, however, the groove which passes forwards to the mantle-edge beneath the rectum is lined with a cubical epithelium, similar to that of the ureter itself.

The Central Nervous System is shown in Fig. 4 on Plate VI. The buccal mass is capable of being withdrawn through the nerve-ring, the cerebral ganglia and commissure being situated immediately above the jaw in the specimens examined. The cerebral ganglia are united by a commissure measuring about ·25 mm. in length. The projecting anterior portion of each ganglion bears a small lateral lobe on its outer side. The buccal ganglia are situated behind the

opening of the œsophagus, and are joined to the cerebral ganglia by long connectives. Like the latter ganglia, they do not appear to present any unusual features.

The ventral ganglia are joined to the cerebral ganglia by cerebro-pedal and cerebral-pleural connectives of moderate length, and form a compact group which is more nearly symmetrical in appearance than is usually the case. The ventral group consists of a pair of rounded pedal ganglia in front, and close behind them what at first sight seems to be a single pair of pleuro-visceral ganglia. This appearance is due to the right parietal ganglion being completely fused with the right pleural ganglion, and the left parietal completely fused with the abdominal ganglion on one side and almost completely with the left pleural ganglion on the other.

The otocysts are situated on the ventral surface of the pedal ganglia, near their posterior ends. Each otocyst contains a number of oval otoconia, with deeply staining centres. The otoconia vary considerably in size, but many of them attain a maximum diameter of ·01 mm.

The distribution of the various nerves does not seem to exhibit any marked difference from that usually found in the Helicidæ; but time has not permitted the detailed examination of the smaller nerves and arteries of this species, structures which could be better studied in some larger member of the genus.

The Digestive System.—The jaw measures about ·75 mm. in breadth; it is of a rather light brown colour, and is crossed by twelve to fourteen broad vertical ribs, as shown in Fig. 7 on Plate VI.

The radula is rather narrow, measuring about 1·9 mm. × ·6 mm. when flattened out. The transverse rows of teeth are nearly straight, though they trend slightly forwards in the region of the outer marginal teeth, and to a less extent also in the region of the inner lateral teeth. The central teeth are tricuspid, having a small ectocone on each side of the mesocone. The lateral teeth are bicuspid, there being a short ectocone in addition to the much larger mesocone, which, however, is shorter than the basal plate. The endocone is represented by a small flange on the inner side of the mesocone, to which it is wholly united. In the transitional teeth the distal end of the endocone becomes separated from the mesocone, and the ectocone is not so short. In the marginal teeth the endocone is more prominent, and is only united with the mesocone for about half its length; while the ectocone is usually divided into two small cusps, or even into three in one or two of the teeth. The marginal teeth are much shorter than the others, especially near the edges of the radula; but the forms of the teeth will be seen from Fig. 8 on Plate VI. The following are the radular formulæ of two specimens examined: (14+9+1+10+14)×116; (14+10+1+11+14)×110.

The extremity of the radula-sac projects as a small papilla beyond

the hinder end of the buccal mass. The odontophoral support is composed of radial fibres possessing elongated nuclei, with polygonal cells interspersed between them.

The œsophagus arises from the middle of the upper surface of the buccal mass, and is rather broad, especially in the region of the salivary glands. These glands are irregular in form, and are united with each other above the œsophagus, except towards their anterior ends. Their ducts, which are not quite so long as usual, open into the cavity of the buccal mass on each side slightly below the opening of the œsophagus. Passing backwards, the œsophagus leads into the long stomach which extends round a single whorl. The intestine arises from the hinder end of the stomach, and runs forwards almost to the posterior end of the pericardium, where it bends upwards and backwards, describing the usual S-shaped curve before passing forwards as the rectum to the anus. The course of the alimentary canal is shown in Fig. 9 on Plate VI.

The liver is divided as usual into two separate portions. The posterior one occupies the upper whorls beyond the stomach ; the opening of its hepatic duct is shown in the figure. The anterior division lies in the region of the intestine, the loops of which tend to subdivide it into three lobes, one occupying the lower loop, another the upper loop, while the third is chiefly situated behind the upper loop, but has a narrow prolongation which extends forwards above it.

The Retractor Muscles.—Excepting towards their anterior ends the main retractor muscles are closely coiled in a spiral manner around the columella of the shell. When the muscles are spread out, as shown in Fig. 3 on Plate VI, it is seen that the columellar muscle divides close to its origin into an upper and a lower portion. The latter is the broad retractor of the hinder part of the foot. The upper portion soon divides again into a right and a left branch, and a little further forwards the left branch again divides into an upper and a lower muscle. The upper muscle is the powerful buccal retractor, which becomes subdivided into several strands close to its insertion in the buccal mass. This muscle appears to be innervated by a pair of very slender nerves arising from the cerebral ganglia. The lower left muscle unites with a strand arising from the right branch, and passes forwards, eventually dividing into the upper and lower left tentacular retractors and a couple of muscles to the left side of the anterior end of the foot. The right branch, after giving off the muscle that unites with the left branch, also passes forwards, and divides into the retractors of the upper and lower right tentacles and of the right side of the anterior end of the foot. These retractors all lie on the left of both the male and female genital ducts. The muscular strand that passes from the right to the left cephalic retractor in front of the origin of the buccal retractor, is not an abnormality, as

it occurs in all of the three specimens in which these muscles were examined ; moreover, it is also found in other Helicid genera, such as *Helicella*.

The penial retractor arises from the diaphragm, or floor of the mantle-cavity, towards its anterior end, and is attached to the epiphallus about ·5 mm. behind the penis.

The Reproductive Organs are shown in Fig. 5 on Plate VI. The hermaphrodite gland or ovotestis is deeply embedded in the posterior division of the liver, and, being unpigmented, its exact form is difficult to make out. The hermaphrodite duct is very slender for at least half of its length, but a little in front of the middle it is slightly swollen and convoluted, though less so than in many other snails. It bends abruptly backwards on entering the albumen gland, and forms a very rudimentary vesicula seminalis. The albumen gland is large and elongated, its hinder part being concave on the inner side where it lies against the stomach. The spermoviduct or common duct is divisible, as usual, into the female side, with glandular, semi-translucent, transversely folded walls, and the male side, covered by the long and rather narrow, opaque-white prostate gland.

The free oviduct is rather narrow and not very long. The receptaculum seminis or spermatheca is an oval sac which lies close to the female side of the spermoviduct not far from the middle of its length. It sometimes contains an irregular hard brown mass. The receptacular duct is of moderate length, and is without any diverticulum. The free oviduct and the receptacular duct open together into a broad vagina. From the posterior end of the lower surface of the vagina three small finger-shaped processes arise close together. These processes measure about ·1 mm. in diameter, and vary in length ; the longest, however, does not exceed 1 mm. in length, while the shortest of the three is usually less than half the length of the others. They are hollow, and are lined by a rather thick epithelium of tall and narrow columnar cells, with elongated basal nuclei. Outside of this epithelium there is a layer of circular muscle-fibres, but no glandular tissue seems to be present, although there can be no doubt that these processes are homologous with the so-called mucous glands found in so many of the Helicidæ. In front of them, on the outer side of the vagina towards its posterior end, there is a conspicuous hemispherical swelling, which is doubtless a degenerate dart-sac. It contains no dart, and the structure of its walls is not unlike that of the posterior part of the vagina itself, being lined by an epithelium of narrow columnar cells, with unusually long and narrow nuclei.

The vas deferens, after separating from the spermoviduct, runs forwards beside the female duct nearly to the genital atrium, and then bends round and passes backwards for about 3·5 mm. Lastly it bends forwards again, and enters the epiphallus, enlarging as it does so. The epiphallus is about 2 mm. in length by ·35 mm. in

diameter, being very thick and muscular. Behind its union with the vas deferens it is continued as an equally thick and muscular flagellum, about 1 mm. long, with a broadly rounded extremity. The epiphallus and the unusually broad flagellum have a similar histological structure. They are lined by a columnar epithelium, which is folded so as to form minute papillæ; next to this there is generally a little connective tissue, but most of the wall consists of a thick outer layer of mixed longitudinal and circular muscle-fibres. The penial retractor muscle, as already mentioned, is attached to the epiphallus towards its anterior end. The penis is nearly 2 mm. long, and is considerably broader than the epiphallus, with a much larger cavity, although its walls are somewhat flattened. It is smooth internally, with a short broad penis-papilla projecting into its hinder end and having the small opening of the epiphallus at its apex, as shown in Fig. 6 on Plate VI. The penis, as well as the other genital ducts, lies on the right side of the retractor of the right upper tentacle. The genital atrium is rather small, but a few scattered gland-cells are contained in its wall.

(2) The Affinities of *Ochthephila*.

In 1895 Pilsbry placed the genus *Ochthephila* or *Geomitra* next to *Helicella* among the Siphonadeniate Helicidæ, although he did so with some doubt, and said: "it would obviously be quite idle to discuss the origin or genesis of this genus until its anatomy is made known."[1] Recently Cockerell dissected a specimen of *O. pulvinata* (Lowe) from Porto Santo, and found that it had no dart-sac or mucous glands; he therefore suggested that the genus belonged to the Epiphallogona, and that "*Ochthephila* represents a survival of a type of Helicidæ which is now mainly developed in the Oriental and Australian regions".[2] He added, however, that he had found in *O. pulvinata* a slender cylindrical organ closely resembling, on a small scale, the supposed degenerate dart-sac of *Theba cantiana*, and wrote: "If this structure is really a degenerate dart-sac, then *Ochthephila* may be a member of the Belogona which, through degeneration, simulates the Epiphallogona."

It will be seen from my description and figures of the anatomy of *Ochthephila turricula* (Lowe) that Cockerell's second suggestion is undoubtedly the correct one, for this species possesses both a dart-sac and mucous glands, though in a very degenerate condition. Further, it appears that Pilsbry could not have done better than place this genus next to *Helicella*, with which it seems to have close affinities.

Ochthephila turricula closely resembles *Helicella* and *Theba* (which Pilsbry regarded as a subgenus of *Helicella*) in the external features of the animal, in the form of the kidney, in the central nervous system, in the retractor muscles, in the position of the penis on the

[1] *Man. Conch.*, ser. II, vol. ix, p. 238.
[2] *Journ. of Conch.*, vol. xvi, 1922, p. 311.

right of the right ocular retractor, in the well-developed epiphallus and short flagellum, in the position of the degenerate mucous glands, and in the unbranched receptacular duct of moderate length. Moreover, the degeneration of the dart apparatus occurs also in these genera, especially in *Theba*, culminating in the entire absence of these organs in *Ashfordia granulata* (Alder). The jaw of *Ochthephila turricula* is intermediate in type between that found in *Theba*, in which there are usually a rather larger number of ribs, and that found in *Helicella*, in which the number of ribs is generally smaller.[1] The radula is also of the same type, although in the larger or more specialized species of these genera the endocone often becomes completely united with the mesocone in the marginal, as well as in the lateral teeth. Even in the shell some species of *Ochthephila*, such as *O. michaudii* (Dh.), closely resemble *Helicella*, although this cannot be said of the species here described. Almost the only anatomical character that seems to separate *O. turricula* from *Helicella* and the other European Helicids is the very broad and obtuse form of the flagellum, and it remains to be seen whether this feature is a constant character of the genus ; Cockerell states that in *O. consors* (Lowe) " the stout flagellum ends in a nipple-like papilla",[2] but he gives no figure of it.

Thus it would seem that the affinities of the genus *Ochthephila* are with *Helicella* and *Theba*, genera which are usually regarded as rather closely allied to each other. Hesse, however, considers that *Theba* is related to *Hygromia* rather than to *Helicella*, notwithstanding the different position of the right ocular retractor, chiefly because *Theba* more nearly resembles *Hygromia* in the coloration of the shell and mantle.[3] But this character does not seem to be of much importance, being largely dependent on the environment. We find, moreover, that in some species of both *Hygromia* and *Theba* the shell is semi-opaque with brown bands, and it is not unlikely that in the common ancestor of all the genera the shell was not more conspicuously striped than in these species. If this be the case, it would

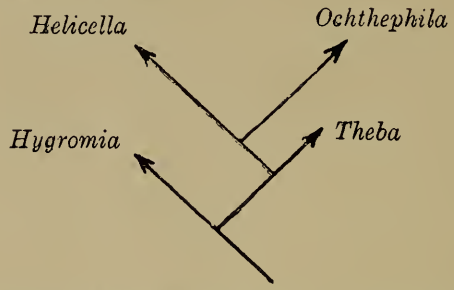
[1] According to Pilsbry (op. cit., p. 238) and Cockerell (*Proc. Malac. Soc.*, vol. xiv, 1921, p. 195) in *Ochthephila* (*Hystricella*) *bicarinata* (Sow.) and *O.* (*Discula*) *polymorpha* var. *discina* (Lowe) the jaw has but ten ribs, while in *O.* (*Plebecula*) *lurida* (Lowe) it has only eight, being thus of the type found in *Helicella*. On the other hand, Pilsbry states that the jaw of *O.* (*Caseolus*) *abjecta* (Lowe) has no ribs at all.

[2] *Journ. of Conch.*, vol. xvi, 1922, p. 311.

[3] *Archiv für Molluskenkunde*, vol. liii, 1921, p. 56. Hesse also mentions a possible difference between *Theba* and *Helicella* in the pallial lobes near the respiratory opening ; but an examination of these lobes shows that they are very similar in *Hygromia*, *Theba*, *Helicella*, and *Ochthephila*.

It should be explained that in the present paper the names *Hygromia* and *Helicella* are employed, in the way in which they are used by Pilsbry and others, for the genera of which *H. cinctella*, Drap. and *H. itala*, Lin. are the respective types ; for I have given reasons elsewhere (*Journ. of Conch.*, vol. xvi, 1922, pp. 277, 279) for believing that this usage is in accordance with the International Rules of Zoological Nomenclature, notwithstanding recent suggestions to the contrary.

be simplest to suppose that the change in the position of the ocular retractor took place first, before *Theba* branched off from the ancestors of *Helicella* and *Ochthephila*, and that the greater opacity of the shell found in most species of the latter genera, and the consequent reduction in the pigmentation of the mantle, were features which arose later, owing to the preference of these snails for less shady situations. Nevertheless, Hesse is probably right in regarding *Hygromia* and *Theba* as closely related, for all these genera seem to be nearly allied to one another. Possibly their mutual relations may be somewhat as follows :—



The microscopical sculpture of the shell of *Ochthephila turricula* and allied species closely resembles that of the type species of *Helicigona*, but the anatomy of the two genera shows that this resemblance is not due to any close relationship between them. Indeed, it is doubtful whether the reproductive organs of any European genus belonging to the Helicidæ are more unlike those of *Ochthephila* than are these organs in *Helicigona*. The larger Siphonadeniate Helicids—i.e. *Helix*, *Helicigona*, etc.—seem to belong to a slightly different and somewhat more primitive group than the genera dealt with above. In them the kidney appears to be of a slightly different shape, with the mantle-cavity extending further back above it, both the pleural ganglia are still quite separate from the parietal ganglia, the long receptacular duct usually bears a diverticulum, and the dart-sac and mucous glands have not yet become more or less degenerate. But it is possible that the smaller Helicids have not been directly derived from any of the larger genera now existing; it is even conceivable that they may have been independently evolved from the Euadenia; for the step is not a great one, and some of the Euadenia, such as the African genus *Halolimnohelix*, seem to resemble *Hygromia* and its allies in some respects more closely than the latter genera resemble the larger European Helicids. Probably a comparative study of the central nervous system in these various forms would throw some light on their probable relationships, but unfortunately nothing has yet been published about the nervous system of *Halolimnohelix* and many other genera.

It is generally agreed that the Molluscan fauna of the Madeira